

CRANIODENTAL VARIATION OF MACAQUES (*Macaca*): SIZE, FUNCTION AND PHYLOGENY

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Abstract: In order to analyze skull variation in the genus *Macaca*, seventy-seven craniodental variables were taken from eleven species. They were first defined seven functional units comprising three anatomical regions. Twenty-seven variables were finally selected to carry out the morphology of the whole skull. The data, organized in these ways, were examined to discover variations between and within the various species. The methods used were Principal Components Analysis (PCA) and Discriminant Function Analysis (DFA). PCAs of the functional units anatomical regions, and the whole skull provided similar, though not identical, separations of species clusters in both sexes separately. These differences in structure could be related to size, sexual dimorphism, diet, ecology, classification and phylogeny. The question of size should have been easy to settle. Unfortunately, this is not the case. In this study where the raw data are measurements of the specimens, the main differences should be size. However, the size differences seem to occur in both the first and second (independent) multivariate axes. In some analyses the size differences between the species are biggest and appear in the first axis. In other analyses it is the separation between the sexes (and these too are largely size) that are the biggest and appear in the first axis. Yet in other analyses, both of these size separations, though still orthogonal to one another, present in the combination of the first two axes. This certainly implies that a single axis of body size is not present and that shape differences have not been isolated from size differences. It also implies that sexual dimorphism is a complex matter. As a result, the question of the relationships between the species is therefore also complex. One cluster of species that includes *M. fascicularis*, *M. sinica* and *M. radiata* was significantly isolated from all others regardless of level of analysis. This relationship is quite different from that proposed on the anatomy of the reproductive organs (Delson, 1980; Fooden, 1976, 1980).

Key words: Primates; *Macaca*; Craniodental variation; Morphometric analysis; Functional adaptation; Phylogeny

There have not been many craniodental morphometric studies of macaques (Pan, 1998; Pan *et al.*, 1998). Such results as there are suggested that the studies provide an excellent anatomical system with which to test hypotheses of morphological integration and classification. Some results were also useful in revealing the relationship between craniodental morphology and its underlying developmental bases^③. Questions still remain to be tested. To what extent can phenotypic results provide evidence clarifying controversies about phylogeny? To what degree can variation between species be separated in association with functional adaptation and phylogenetic inertia?

Phylogenetically, macaques have been categorized into four species-groups but with different definitions based on the morphology and structure of the reproductive organs (Delson, 1980; Fooden, 1976, 1980). These concepts have been tested by results from other research fields, for instance, fossil records and external features (Eudey, 1980), biological and karyological studies (Fooden *et al.*, 1989; Melnick *et al.*, 1985; Zhang *et al.*, 1990), and behaviour (Chan, 1996; Fooden, 1975).

Regarding differences in functional adaptation, a detailed comparison of diets and ecology of macaque species was provided by DeClue *et al.* (1992). The

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③Pan and Oxnard, in preparation

various species have been described as adapted to a wide variety of habitats and living conditions, and as displaying an extensive range of diets and feeding behavior. These variations might be relevant to corresponding species differences in morphologic structure of the teeth and cranium. A limited study of this type has been undertaken by Hylander (1979) and Takahashi *et al.* (1994).

The study aim is to provide further tests using craniodental morphometric analysis with a large number of variables and species. This study attempts to do this by examining craniodental variation at three distinct levels of anatomical organization, individual functional units, anatomical regions and the whole skull. Implications for functional adaptation and phylogenetic relationship will be examined.

1 Materials and Methods

Eleven species of the genus *Macaca* (Table 1) were used in this study. The materials are housed in a number of institutes, universities and museums in various parts of the world (see Acknowledgments). All specimens were from adult macaques as judged by the full eruption of M3s. They were of wild shot animals or of animals that had died of natural causes.

Seventy-seven linear dental, mandibular and cranial variables (Table 2) were measured on each specimen using digital calipers. Length measurements were made parallel to the median sagittal plane, and breadth (or width) measurements were made in the coronal

plane. Heights were measured at the right angles to length and breadth.

Principal Components Analysis (PCA) was applied to the resulting data. Clusters of major contributing variables were identified using, as a significance criterion, minimum loadings of 0.300 (Hair, *et al.*, 1992). The variables were studied in three successive steps to focus on different anatomical aspects. In the first step variables were grouped into 7 units on the basis of function. Some variables were selected and divided into three anatomic regions secondly. Twenty-seven variables were finally used to analyze the morphology of the whole skull. This division of skulls into three investigational levels: functional units, anatomical regions and the skull as a whole, was aimed at investigating the ways in which the different parts with different functions separate the sexes and the species^① (Pan, 1998).

Since a big sample size from 11 species of the genus *Macaca* was used in this study, it will be difficult in figuring out the separation between species if all individuals were plotted on diagrams of PCA and DFA. So only means of loading scores of each sex or species were shown.

2 Results

Eigenvalues and eigenvectors for each analysis of each individual sex were provided. Those for the sexes taken together are not listed since both the name and number of the variables making significant contributions to the first two axes were very similar either to females or males taken separately.

2.1 Principal Components Analysis

2.1.1 Functional units

Seven units, the mandible, lower teeth, upper teeth, lower face, upper face, cranium and the calvaria, were analyzed separately by PCA. In these initial comparisons, the patterns of separations of the species and the sexes are used heuristically in order to increase understanding of the effects of analyzing the different anatomical regions.

① Females The separations between species de-

Table 1 Species and number (by sex) used in this study

Species	Male	Female	Unknown	Total
<i>M. mulatta</i>	20	20		40
<i>M. fuscata</i>	11	11		22
<i>M. sinica</i>	14	8		22
<i>M. assamensis</i>	20	20		40
<i>M. radiata</i>	12	12		24
<i>M. arctoides</i>	20	20		40
<i>M. sylvanus</i>	11	10		21
<i>M. nemestrina</i>	20	20		40
<i>M. nigra</i>	8	8		16
<i>M. fascicularis</i>	20	20		40
<i>M. thibetana</i>	11	8	1	20
Total	167	157	1	325

① Pan and Oxnard, in preparation

Table 2 Percentage of total variation, eigenvalues and eigenvectors for the first two PCA axes for variables of functional units in the female macaques

Mandible			Lower teeth			Upper teeth		
	1	2		1	2		1	2
Eigenvalue	10.94	1.46	Eigenvalue	9.64	1.66	Eigenvalue	10.68	1.33
Percentage	68.4	9.1	Percentage	60.3	10.4	Percentage	66.7	8.3
Cum. per	68.4	77.5	Cum. per	60.3	70.6	Cum. Per	66.7	75.0
Eigenvectors			Eigenvectors			Eigenvectors		
LBCB	0.682	0.619	LI1MDL	0.249	0.921	UI1MDL	0.458	0.637
LBMB	0.936	0.089	LI2MDL	0.562	0.707	UI2MDL	0.647	0.423
LI1AW	0.430	0.791	LCMDL	0.509	-0.310	UCMDL	0.769	0.147
CONDYLL	0.549	-0.281	LP3MDL	0.701	-0.211	UP3MDL	0.851	0.040
CONDYLW	0.884	-0.201	LP4MDL	0.888	0.099	UP4MDL	0.885	-0.156
CONMI	0.956	-0.143	LM1MDL	0.875	0.166	UM1MDL	0.859	-0.214
CONM3	0.877	-0.221	LM2MDL	0.929	-0.084	UM2MDL	0.901	-0.194
MAMI	0.863	-0.296	LM3MDL	0.909	-0.186	UM3MDL	0.891	-0.196
MAT	0.725	-0.132	LI1BLL	0.623	0.002	UI1BLL	0.620	0.569
MANDLAL	0.896	0.011	LI2BLL	0.741	-0.071	UI2BLL	0.764	0.310
MANDH	0.899	-0.070	LCBLL	0.544	0.160	UCBLL	0.814	-0.020
MANDSYM	0.896	0.172	LP3BLL	0.845	0.066	UP3BLL	0.867	0.043
BICONDY	0.955	-0.144	LP4BLL	0.914	-0.091	UP4BLL	0.866	-0.056
MANCORWI	0.863	-0.068	LM1BLLM	0.900	-0.062	UM1BLLM	0.895	-0.263
SYMWID	0.884	0.055	LM2BLLM	0.935	-0.136	UM2BLLM	0.926	-0.214
LTRLALV	0.728	0.296	LM3BLLM	0.896	-0.148	UM3BLLM	0.904	-0.186

Maxilla			Cranium			Calvaria			Upper face		
	1	2		1	2		1	2		1	2
Eigenvalue	4.64	0.72	Eigenvalue	6.10	0.96	Eigenvalue	4.30	0.98	Eigenvalue	5.64	0.71
Percentage	77.4	11.9	Percentage	76.3	12.1	Percentage	61.4	14.0	Percentage	70.6	8.9
Cum. Per	77.4	89.3	Cum. Per	76.3	88.3	Cum. Per	61.4	75.5	Cum. Per	70.6	79.5
Eigenvectors			Eigenvectors			Eigenvectors			Eigenvectors		
MUZL	0.926	-0.107	BCRANL	0.951	-0.028	CALVL	0.926	-0.117	MUZL	0.863	-0.039
PALLEN	0.959	-0.109	CRANL	0.980	0.015	BPORW	0.911	-0.117	BIORBW	0.837	0.181
PALWID	0.905	-0.143	CRANW	0.909	0.162	MIDPARW	0.895	-0.040	INTORBW	0.726	0.633
UBCB	0.914	-0.070	BLZYGW	0.934	-0.062	POSTORB	0.618	0.397	PIRH	0.861	-0.027
UBMB	0.933	-0.081	POSTORB	0.557	0.689	OCCH	0.594	-0.663	PIRW	0.755	-0.476
UIAW	0.582	0.812	OCCH	0.567	-0.674	FORMAGL	0.550	0.590	UFACEH	0.848	-0.197
			ANTBASI	0.976	-0.041	FORMAGW	0.880	0.085	INFRMAL	0.905	0.062
									BIZYGW	0.908	-0.092

The variables reaching significant contribution level are in bold. For the definition of variables please see Pan, 1998; Pan, *et al.*, 1998.

fine primarily three clusters and are mainly seen along the first axis (Fig.1). Except for some overlap between the second and the third clusters in the upper face, this finding is clear. (The number of species in the studies involving units in the mandible is one less than in the other regions because of missing data for *M. nigra*). To facilitate comparisons, three clusters of species are outlined by convex polygons in the diagrams. These polygons are not assumed, at this point, to have any biological meaning with regard to the species clustering, but rather as providing a guide to the differential patterns produced by the different anatomical areas. In other words, the polygons are here a heuristic device for revealing similarities in the results in the different levels of analysis. The first cluster (polygon) includes the species *M. fascicularis*, *M. radiata* and *M. sinica*; the

second, the species *M. assamensis*, *M. nemestrina*, *M. mulatta* and *M. nigra*; and the third, the species *M. arctoides*, *M. thibetana*, *M. fuscata* and *M. sylvanus*.

The first two axes in each study account for more than 70.0% of the total variation (Table 2). In PC1 only one variable, LI1MDL, does not show a significant positive contribution. In the second axis the variables showing significant positive contributions are LBCB, LI1AW, LI1MDL, LI2MDL, UI1MDL, UI2MDL, UI1BLL, UI2BLL, UIAW, POSTORB, FORMAGL and INTORBW. Those with significant negative contributions are LCMDL, OCCH and PIRW.

②Males Again, in general terms the same three clusters of species are evident. In contrast with the situation in females, there is somewhat greater overlap a-

among these clusters in four units: lower teeth, lower face, cranium and the calvaria. In general, the separation between clusters is similar to that in females although individual separations are smaller (Fig. 2).

In males, more than 66.7% of the total variation is accounted by the first two axes. As with females, all variables in PC1 show significant positive contributions (Table 3). The variables showing significant positive contributions to PC2 include LBCB, LIAW, LTRLALV, LI1MDL, LI2MDL, LCMDL, LP3MDL, LI1BLL,

LCBLL, UI1MDL, UIAW, OCCH, FORMAGL, FORMAGW, UCMDL, UCBLL, BIORBW and INTORBW. Those with significant negative contributions are MAM1, LM2MDL, LM3MDL, LM1BLLM, LM2BLLM, UBMB, POSTORB, OCCH, MUZL, PIRW and UFACEH.

③Two sexes together The analysis of the sexes taken together are illustrated in Fig. 3. Three patterns of variation were found. The first pattern is in the mandible, lower teeth and the upper teeth, in which the

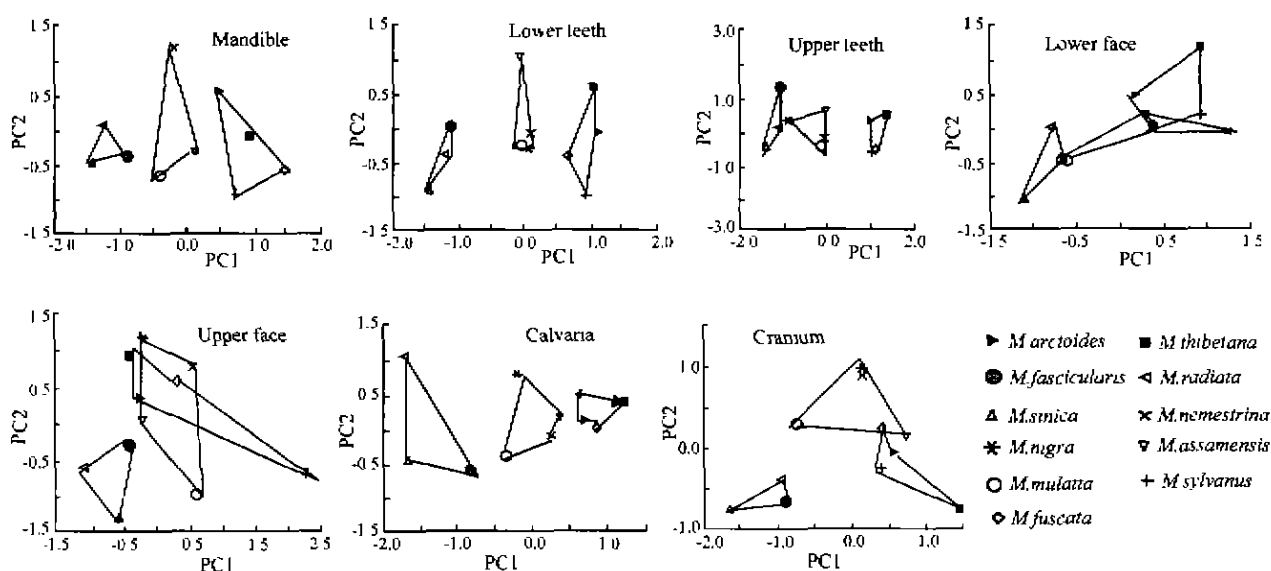


Fig. 1 Plots of the first two principal components of the analyses of individual functional units in female macaques

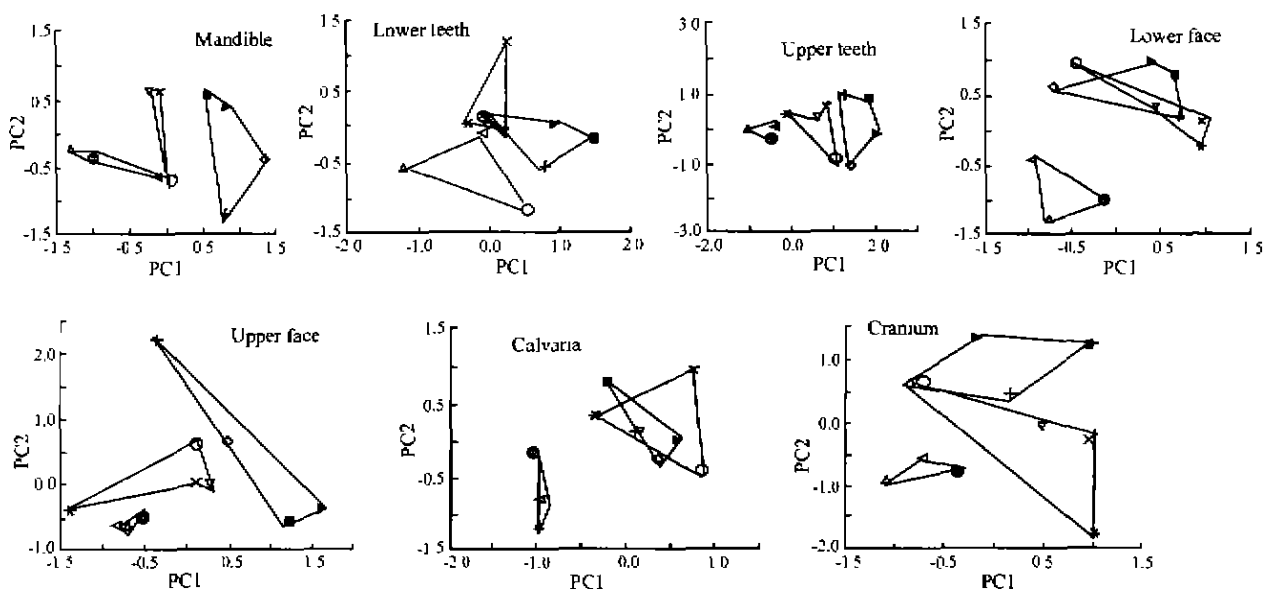


Fig. 2 Plots of the first two principal components for functional units in male macaques

Table 4 Percentage of the total variation, eigenvalues and eigenvectors for the first two principal components in the three anatomic regions

Masticatory apparatus									
	Female		Male			Female		Male	
	1	2	1	2		1	2	1	2
Eigenvalue	15.50	2.53	15.02	57.80	UP4MDL	0.883	-0.056	0.859	-0.259
Percentage	59.6	9.7	2.71	10.4	UM1MDL	0.831	-0.028	0.862	-0.275
Cum. Per	59.6	69.4	57.8	68.2	UI1BL	0.633	0.258	0.487	0.630
Eigenvectors					UI2BL	0.773	0.153	0.760	0.067
LBCB	0.736	0.059	0.792	0.258	UCBL	0.767	-0.103	0.656	0.248
LBMB	0.914	-0.227	0.888	-0.219	UP4BL	0.872	-0.012	0.831	-0.154
LIAW	0.615	0.453	0.666	0.504	UM1BLM	0.898	-0.094	0.823	-0.394
CONM1	0.868	-0.379	0.853	-0.164	LI1MDL	0.348	0.803	0.476	0.734
MAM1	0.742	-0.468	0.689	-0.211	LI2MDL	0.630	0.505	0.626	0.260
MANDLALV	0.887	-0.330	0.883	-0.021	LCMDL	0.525	-0.226	0.597	0.168
MANDH	0.819	-0.312	0.881	-0.015	LP4MDL	0.922	0.065	0.861	-0.090
BICONDYL	0.864	-0.355	0.883	-0.211	LM1MDL	0.856	0.130	0.812	-0.234
UI1MDL	0.531	0.606	0.606	0.608	LCBLL	0.543	0.204	0.560	0.263
UI2MDL	0.719	0.278	0.744	-0.126	LP4BL	0.886	0.041	0.861	-0.202
UCMDL	0.793	0.073	0.729	0.341	LM1BLM	0.854	0.009	0.805	-0.364
Cranium as a whole									
	Female		Male			Female		Male	
	1	2	1	2		1	2	1	2
Eigenvalue	7.79	1.20	6.56	1.38	Eigenvalue	7.30	1.00	7.07	1.33
Percentage	59.9	9.2	50.5	10.60	Percentage	66.4	9.1	64.3	12.1
Cum. per	59.9	69.1	50.5	61.1	Cum. per	66.4	75.5	64.3	76.3
Eigenvectors					Eigenvectors				
CALVL	0.953	-0.053	0.872	0.175	MUZL	0.925	0.050	0.893	-0.237
BPORW	0.925	-0.104	0.910	-0.099	BIORBW	0.808	-0.270	0.720	0.528
MIDPARW	0.865	0.006	0.781	-0.386	INTORBW	0.676	-0.340	0.562	0.639
INTRMAL	0.887	-0.243	0.920	0.097	PALLENG	0.994	0.106	0.919	-0.212
POSTORB	0.595	0.598	0.667	-0.197	PALWID	0.864	0.166	0.861	-0.205
TEMFOSL	0.864	-0.058	0.838	0.006	UBCB	0.870	0.204	0.852	-0.351
TEMFOSW	0.842	-0.038	0.762	-0.002	UBMB	0.928	0.091	0.900	0.093
ZYGH	0.703	-0.038	0.650	0.305	UIAW	0.493	0.727	0.699	-0.478
OCCH	0.579	-0.431	0.530	0.335	PIRH	0.832	-0.303	0.814	0.345
FORMAGL	0.496	0.049	0.498	-0.246	PIRW	0.731	-0.253	0.698	0.128
FORMACW	0.824	-0.180	0.367	-0.623	UFACEH	0.830	0.030	0.822	0.028
GLENOL	0.495	0.722	0.303	0.685					
GLNOW	0.834	0.152	0.804	0.059					

The variables reaching significant contribution level are in bold.

teeth were used to carry out this analysis based on the criteria described above.

a. Females The first two axes account for 69.4% of the total variation. The same three clusters of species as in the analyses of separate functional units were found (Fig. 4). The first axis mainly disperses the clusters in order of species size (the species with the smallest and the largest body size are allocated on the most left and right parts of PC1, separately). The first cluster is discrete but the second one partially overlaps with the species in the third cluster. The second axis also arranges the species in order of size. Overall, an intermediate, diagonal, axis would best separate the three clusters in the first two axes.

In the second axis, CONM1, MAM1, MANDLALV, MANDH and BICONDYL, make significant negative contributions, in contrast to four variables, LIAW, UI1MDL, LI1MDL and LI2MDL, which have significant positive eigenvectors (Table 4). In other words, the anterior teeth play a particular role in the separations in the second axis.

b. Males The first two components account for 68.2% of the total variance (Table 4). The separation among the three clusters in the first axis is not as clear as in the females (Fig. 4) although, again, the first cluster is well separated from the other two. However, quite differently from females, the separation between the clusters is ambiguous in the second axis as there is al-

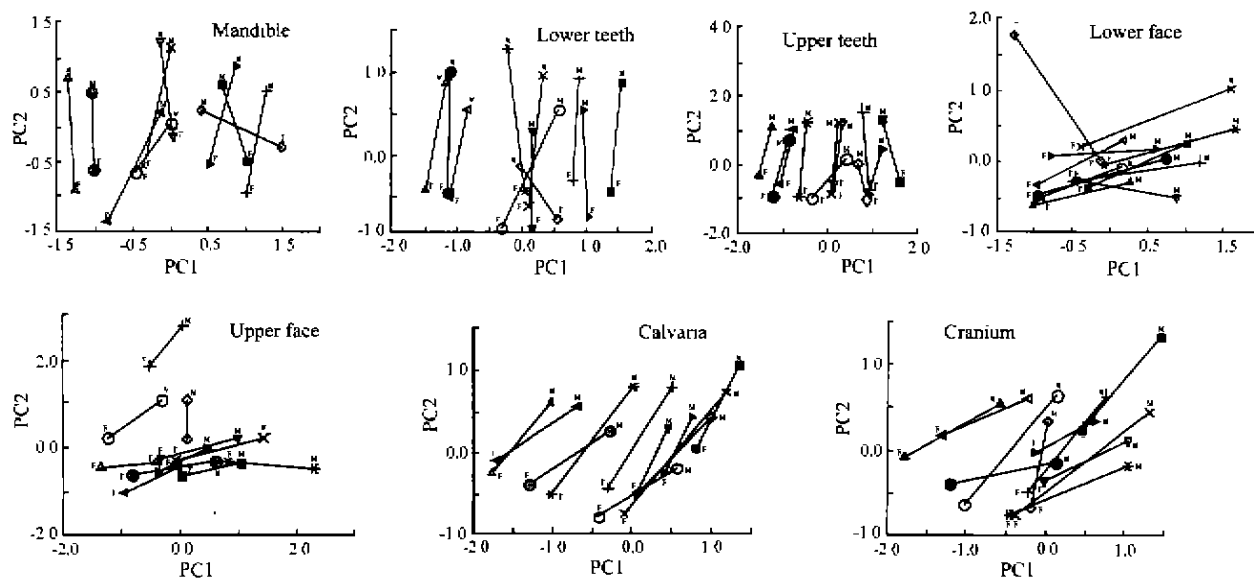


Fig.3 Differences between sexes and species on the first two principal components of the analyses of functional units

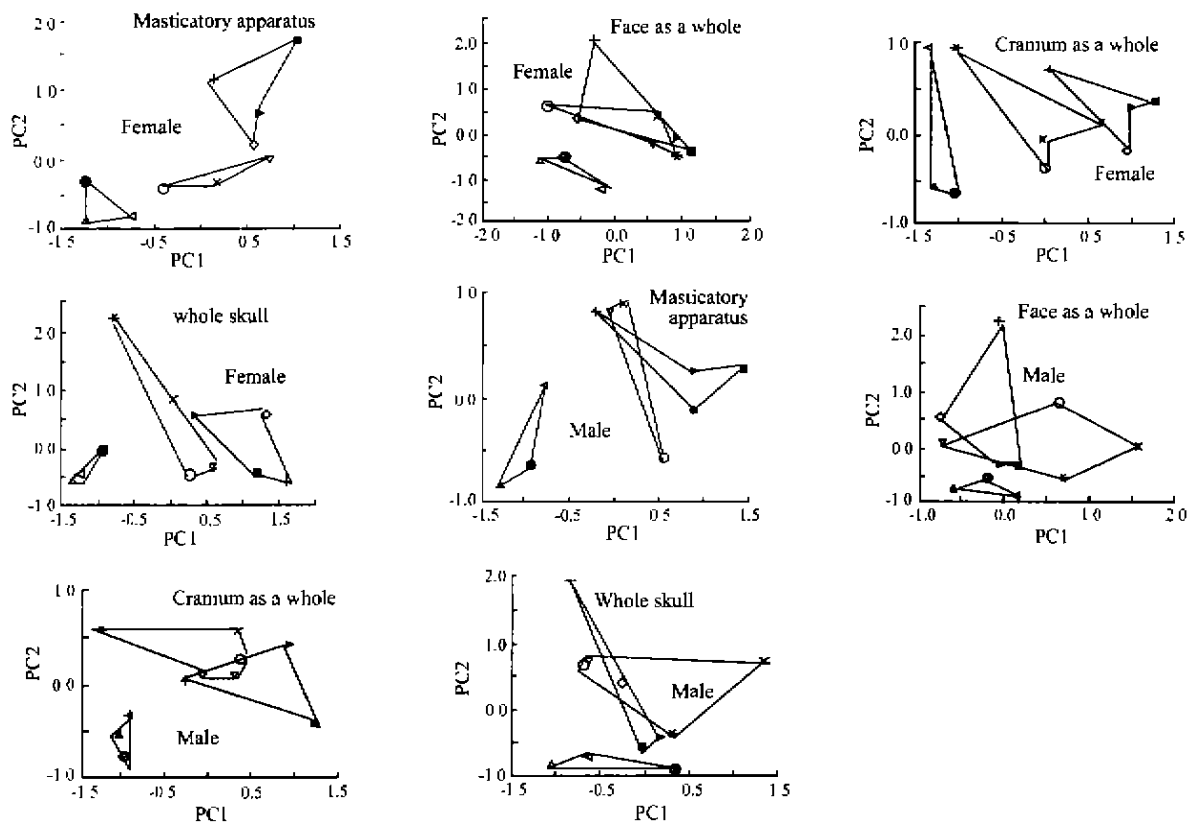


Fig.4 Plots of the first two principal components based on analyses of anatomical regions and of the whole skull

most complete overlap between the three clusters.

Fewer variables than in the females make significant contributions to the second axis. As with females, however, the variable showing the greatest eigenvectors

are positive. They include LIAW, LI1MDL, UI1BLL, LI1MDL, UI1MDL and LI2MDL. All are anterior dental dimensions as in females. The variables making negative contributions have relatively low eigenvectors, only

two of the dental dimensions, UM1BLM and LM1BLM, are significant.

c. Females and males The separation between species in PC1 is almost solely due to the body size of species (Fig. 5). The difference between the sexes within species is virtually totally in the second axis. These patterns are very similar to those obtained from the various functional units.

②Cranium as a whole Thirteen variables were chosen from the cranium and the calvaria for this analysis based on the criteria already presented.

a. Females The eigenvalues and eigenvectors for these analyses are listed in Table 4. The first two axes account for 69.1% of the total variation. The first cluster is yet again well separated from the other two which overlap partly. The dispersion of species in the second axis is similar to that of the calvaria analysis. That is, the three clusters overlap completely.

In PC2 the positive eigenvectors, the breadth of the postorbital constriction (POSTORB) and glenoid length

(GLENOL), are contrasted mainly with the negative eigenvector, the occipital height (OCCH).

b. Males The first two components constitute 61.1% of the total variation (Table 4). The arrangement of the clusters is somewhat similar to that of the cranium (Fig. 2 and 4); the three species in the first cluster are significantly separated from the rest of species and there is a strong overlap between the second and third clusters.

The variables making significant positive contributions to the second component are ZYGH, OCCH and glenoid length (GLENOL) and foramen magnum breadth (FORMAGW). INFRMAL and FORMAGW make significant negative contributions to this axis.

c. Females and males The separation between sexes is in the first axis, and that between species is in the second axis (Fig. 5). The three species, *M. radiata*, *M. sinica* and *M. fascicularis* are very closely grouped and significantly separated from the rest of the species along the second axis. *Macaca thibetana*

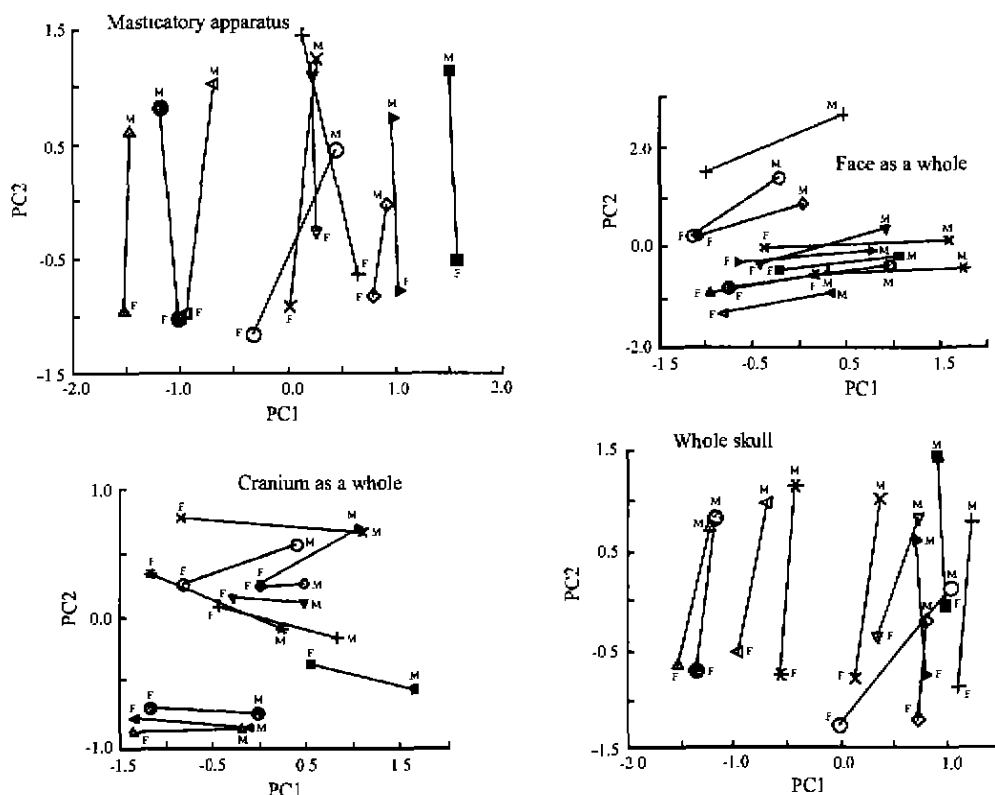


Fig. 5 Differences between sexes and species on the first two principal components of the analyses of three anatomical regions and the whole skull

shows a unique position in the second axis.

③Face as a whole Eleven variables were selected from the lower and the upper face for this analysis.

a. Females The eigenvalues and eigenvectors are listed in Table 4. The first two components account for 75.5% of the total variance. The separation and the arrangement of the clusters are rather different from those of the lower face, but somewhat similar to those of the upper face (Fig. 1 and 4). The three clusters all overlap totally in PC1. Some separation between clusters is found in the second axis where the first cluster is separated from the other two which strongly overlap (Fig. 4).

The variables showing significant negative contributions to the second axis are the interorbital breadth (INTORBW) and the height of the piriform aperture (PIRH). Only one variable has a significant positive contribution, the maxillary incisor alveolar breadth (UIAW).

b. Males The first two components account for 76.3% of the total variation. Overall, the arrangement of the clusters in the two axes is rather different from that of either of the individual units (Fig. 2 and 4). The dispersions of the clusters in the first axis, however, are very similar to that of the lower face; there is strong overlap between all three clusters. In PC2 the first clus-

ter is separated from the other two which strongly overlap.

Biorbital breadth (BIORBW), interorbital breadth (INTORBW) and PIRH have significant positive eigenvectors and are contrasted with UBCB and alveolar breadth (UIAW) which make significant negative contributions to the second axis. These variables, as in females, are mainly linked with the anterior breadths.

c. Females and males The difference by sex within species lies mainly in the first component (Fig. 5), that between species, however, is in the second axis. Both of these differences are primarily related to size (the main difference between both species and sexes) but in this case, the effect of size between sexes is the larger. This pattern is quite similar to those of the individual units (Fig. 3) but clearer and with fewer exceptions.

2.1.3 The whole skull

Twenty-seven variables were selected from the three anatomic regions to cover the morphology of the whole skull (Table 5). These variables were selected from those making the greatest significant contributions in the first two axes, whilst considering the balance between the various regions. All PC1 eigenvectors are significantly positive, and the other axes include both positive and negative eigenvectors.

Table 5 Percentage of the total variation, eigenvalues and eigenvectors in the first two principal components based on the analyses of the whole skull

	Female		Male			Female		Male	
	1	2	1	2		1	2	1	2
Eigenvalue	14.72	3.46	12.84	3.58	MUZL	0.908	-0.077	0.868	0.162
Percentage	54.5	11.7	47.6	13.2	BIORBW	0.743	-0.184	0.709	-0.382
Cum. per	54.5	66.2	47.6	60.8	INTORBW	0.709	-0.118	0.559	-0.299
Eigenvectors					PALWID	0.846	-0.133	0.871	0.009
LBCB	0.765	0.334	0.834	0.196	UBCB	0.910	0.100	0.827	0.308
LIAW	0.592	0.677	0.683	0.480	UIAW	0.828	0.428	0.723	0.474
CONMI	0.919	-0.197	0.881	-0.256	PIRH	0.793	-0.335	0.758	-0.302
MAMI	0.818	-0.293	0.675	-0.229	CALVL	0.908	-0.253	0.852	-0.355
UI1MDL	0.362	0.761	0.623	0.599	MIDPARW	0.848	-0.247	0.648	-0.492
UCMDL	0.835	0.070	0.743	0.266	INFRMAL	0.888	-0.183	0.878	-0.251
UI1BL	0.581	0.414	0.509	0.603	POSTORB	0.628	0.012	0.700	-0.149
UM1BLLM	0.845	-0.111	0.701	-0.328	OCCH	0.489	-0.154	0.404	-0.239
LI1MDL	0.245	0.839	0.492	0.731	FORMAGL	0.469	-0.162	0.510	-0.423
LI2MDL	0.563	0.575	0.606	0.310	FORMAGW	0.806	-0.249	0.260	-0.336
LCBLL	0.569	-0.006	0.636	0.239	GLENOL	0.553	-0.105	0.492	0.104
LM1BLLM	0.807	0.003	0.707	-0.340					

The variables reaching significant contribution level are in bold.

① Females The total variance accounted by the first two axes is 66.2% (Table 5). In broad terms the first two axes place three of the species in the third cluster (*M. thibetana*, *M. sylvanus* and *M. fuscata*) at the positive extreme, and all species in the first cluster (*M. fascicularis*, *M. radiata* and *M. sinica*) at negative extreme (Fig. 4). This picture resembles the first axis separations of the females in most of the functional units and overall regions (although it is less clear in the face). Overall, this pattern is more like the masticatory region than the others. The second axis seems mainly to just separate individual female of species with no particular pattern evident. The three clusters are significantly separated on the two axes. The variables showing significant positive influences to PC2 are LBCB, LIAW, UI1MDL, UI1BLL, LI1MDL, and UIAW. All of these are anterior dental dimensions. In contrast to these eigenvectors is the height of the piriform aperture (PIRH) which has a significant negative eigenvector (> 0.300).

② Males The first two axes accounted for 60.8% of the total variation (Table 5). In broad terms the first axis contrasts with the picture in the females. There are almost no separations of clusters that resemble those in the various regions in the first axis (Fig. 4). This pattern does not resemble particularly that from any single region (certainly, it is not, as is the case for females, similar to the masticatory apparatus).

The second axis seems mainly to separate the species with no particular pattern evident. More variables than in the females make significant contributions to this axis: Incisor alveolar breadths (LIAW), UI1MDL, UI1BLL, LI1MDL, LI2MDL, UBCB and UIAW are associated with the anterior teeth, and exhibit significant positive contributions. UM1BLL, LM1BLLM, BIORBW, PIRH, CALVL, midparietal breadth (MIDPARW), the length and breadth of the foramen magnum (FORMAGL and FORMAGW) have significant negative eigenvectors; they are mainly associated with breadths of the cranium.

③ Both sexes The first axis separates species by sex according to overall size in a manner extremely similar to the masticatory region (Fig. 5). The differences

between the sexes lay in the second axis, a picture that is very similar to the corresponding axis in masticatory apparatus. This again replicates what is evident in the masticatory apparatus and is quite different from the other regions. However, it is in the remaining significant axes (third and fourth) that this analysis differs from that of the masticatory analysis, these remaining axes performing not inconsequential separations of many individual species.

3 Discussion

Although three species clusters were first used heuristically for defining patterns in the analyses, they do show differences between functional units, anatomical regions and the whole skull. In addition, they all show major differences between the sexes. The variations in craniodental morphology between species or species group have frequently been considered to be associated with both functional adaptation and phylogenetic inertia, and resulting in taxonomic difference (Albrecht, 1976; Cheverud *et al.*, 1986; Harvey *et al.*, 1991; Hylander, 1979).

Macaques are widely distributed from Africa to Asia. They have adapted to a wide variety of ecological conditions and habitats. This high degree of adaptability can be related to a great behavioural and ecological plasticity. Macaques can thus serve as an ideal model to understand the relationship between habitat preferences and variables relating to their past and present evolution, interspecific interaction, and morphology.

Craniodental variation, especially in masticatory apparatus between species might be relevant to adaptation to specific feeding behaviour and dietary components. A significant difference in the masticatory apparatus has been found referring to the primates with different dietary items, especially between the frugivorous and the folivorous species (Hylander, 1979; Smith, 1983; Takahashi *et al.*, 1994). In order to determine whether the variation of craniodental structure between species clusters, especially that in the masticatory apparatus is mainly associated with the differences in functional adaptation or in phylogenetic inertia, it is necessary to examine the information available for the three species

groups.

3.1 The first cluster of species

The species in this cluster include *M. fascicularis*, *M. radiata* and *M. sinica*. They are distributed in Southeastern Asia, India and Sri Lanka. *Macaca radiata* occurs in the low land and high land forests (Simonds, 1965), scrub jungles semi-evergreen forest, bamboo forest and rain forest (Krishnan, 1971; Nolte, 1955) in south of India. Its populations frequently appear on the roadside near agricultural fields (Simonds, 1965). It feeds on wild fruits, flowers, leaves, seeds and other foods from agricultural fields and catch insects and small animals (Rahaman *et al.*, 1969; Krishnan, 1971; Nolte, 1955). In general, its adaptation in the wild is very similar to that of *M. mulatta* (DeClue *et al.*, 1992). *Macaca sinica* is an endemic species to Sri Lanka. It appears in all major forest zones in Sri Lanka, including arid, semi-evergreen transitional, and evergreen forests, from near sea shore to 2 100 meters above the sea level (Fooden, 1979). The diet of this species is variable; they can process foods from as many as 46 plant species (DeClue *et al.*, 1992). *Macaca fascicularis* occurs in a wide variety of habitats in Southeast Asia. Its distribution areas include the forests of tropical evergreen rain forests, riverine, mangrove, monsoon, bamboo, agriculture regions and other areas of scrub and grasslands (Eudey, 1980; Kurland, 1973, Southwick *et al.*, 1972). This species utilises between 20 and 179 plant species. Fruits are the major proportion (about 51% - 55%), so that this species is a good seed dispenser (Lucas, 1996). Leaves, stems, and bracts account for a smaller food proportion (3% - 27%). In some cases insects and animal prey may account for as little as 4% and as much as 23% (DeClue *et al.*, 1992).

3.2 The second cluster of species

The species including in this cluster are *M. mulatta*, *M. assamensis*, *M. nemestrina* and *M. nigra* (when present in the data). These species occupy a large area in Asia. *Macaca mulatta* lives in a wide range of habitats than any other macaques. Its populations occur both in forests with little human intervention and in highly urbanised environments. It is adapted to

deep snowfall, deserts, subtropical, tropical, sparsely vegetated habitats, both coniferous and deciduous forests, and swamps (Fooden, 1982; Southwick *et al.*, 1966, 1968; Zhang *et al.*, 1989). It is highly omnivorous (Lindburg, 1971; Makwana, 1979). In some areas foods include 42.8% fruits, 41.3% leaves and 15.9% flowers (Makwana, 1979), or 63% - 70% fruits (Lindburg, 1971). The distribution of *M. assamensis* includes the evergreen or dry evergreen forests, and bamboo, tropical and subtropical monsoon deciduous forests (Eudey, 1980; Fooden, 1971; Zhang *et al.*, 1989). The diet of *M. assamensis* contains mainly fruits, seeds, invertebrates and vertebrates. The main proportion in some areas, however, are leaves (DeClue *et al.*, 1992; Sarkar *et al.*, 1996). The distribution of *Macaca nemestrina* roughly coincides with that of tropical broadleaf evergreen rain forests (Fooden, 1975) and secondary forests (Southwick *et al.*, 1972). This species is highly frugivorous (Fooden, 1971; Medway, 1970; Rodman, 1978). At Menttoko, it eats fruits from 22 plant species which are overlapped with those eaten by *M. fascicularis* (Rodman, 1991). Thus there is a great similarity in diet between *M. nemestrina* and *M. fascicularis* in some areas. *M. nigra* was seen to raid in maize field and in the tree of the primary forest (Groves, 1980).

3.3 The third cluster of species

The species in this group are distributed in Northern Africa (*M. sylvanus*) and Asia (covering Northern India, Bangladesh, Burma, China, Malaysia, Thailand, Cambodia, Laos, Vietnam and Japan). The vegetation inhabited by *M. sylvanus* is a variety of grasses and herbs with little or no tree or shrub (Ménard *et al.*, 1990), mixed-oak forest (Fa, 1984, 1986), and rocky mountains and forests with a closed canopy and few shrubs (Fa, 1986; Ménard *et al.*, 1996). Foods from cedar trees can account for up 70% of the diet during times of deep snow, or deciduous leaves and herbs in other times (Drunker, 1984; Fa, 1984). The habitats of *M. arctoides* include primary the forests of evergreen, secondary evergreen, hill evergreen, mixed deciduous leaves, and dry rocky outcrops (Bertrand, 1969; Fooden, 1971; Treesucon, 1988). The diet of *M. arctoides*

include fruits, leaves and seeds from a variety of wild plant species and small animals (Bertrand, 1969; Fooden, 1971; Fooden *et al.*, 1985). According to McCann (1933) it is predominantly frugivorous. The habitats of *M. thibetana* are very similar to those of *M. arctoides*. They include subtropical broadleaf evergreen forests, temperate deciduous, and subtemperate mixed coniferous and deciduous forest (Fooden, 1983; Fooden *et al.*, 1985). The diet of *M. thibetana* is composed of fruits, seeds, bamboo shoots and small animals (Xiong, 1984; Zhao *et al.*, 1988). *Macaca fuscata* is distributed only in those parts of Japan covered with the deciduous-broad-leaved and subalpine conifer forest as well as bushes (Iwamoto, 1978; Izawa *et al.*, 1963; Wada *et al.*, 1980). This species, however, is highly opportunistic in selecting its diet, fruits and seeds, over different times of the year and at different locations (Nakagawa, 1989).

From the information provided above, even though the habitats of macaques are variable and there are some preferences in diets referring to different species, there are no great variations in diet between the individual species or clusters species found in this study. Nevertheless, the proportion of different food items in macaques are influenced by many factors, for instance, the diversity and availability of food resources, the required energy to obtain such resources, and physiological and behavioural states (DeClue *et al.*, 1992).

This basic commonality of diet implies that craniodental variation, especially in the masticatory apparatus, found between species clusters in this study may be less relevant to dietary adaptation and more associated with other factors, such as body size (Pan, 1998). It is clear that the species in the first cluster are smallest and those in the third cluster are the largest ones. The species in the second cluster are intermediate. These variations in body size among macaque species have been reported by many other researchers (e.g. Hill, 1974; Napier *et al.*, 1967).

It is not impossible that it is simply body size that might explain the main separation between clusters. The findings in this study indicate that *M. radiata* and *M. sinica*, of the *sinica* group, are widely separated

from *M. arctoides*, *M. thibetana* and *M. assamensis* in the same species group proposed by Delson (1980). The former species are of smaller body size than the latter due to divergent evolutionary pathways and adaptation to different geographical areas and environmental zones (Delson, 1980; Fa, 1989). *Macaca radiata* and *M. sinica* may have undergone dwarfing and as a result share few of their size-based characteristics with their putative group mates.

However, the findings here in relation to differences between the sexes (which are also largely related to differences in overall size in a data set that consists of measurements) imply that size is no a simple matter. For example, these two sets of size differences are largely orthogonal. Either one may appear in the first axis where all contributing variables are positive (this has been suggested to imply size). Both may appear (though oppositely arranged) in each of the first two axes. Further investigation of this size complexity is required.

The relationships between some species revealed in this study are, however, similar to those from other research fields. The two stump-tailed macaque species, *M. arctoides* and *M. thibetana*, are always closely clustered. The close relationship between them, as well as between them and *M. assamensis* (another species in the second cluster), has already been reported in studies based on external morphology (Delson, 1980), genetics (Zhang *et al.*, 1990; Zhang, 1991), biomolecular data (Cronin *et al.*, 1980), craniometry (Albrecht, 1978), the similar incidence of lacrimal fossa (Mouri, 1994) and hair structure (Inagaki, 1996). This species is similar to *M. arctoides* and *M. thibetana* in this study. More details about this is available in Pan *et al.* (1998).

Three other species, *M. fascicularis*, *M. radiata* and *M. sinica*, form one cluster in each of skull analyses and show a great separation from the other two. This may imply that there exist close relationships among them from evolutionary and phylogenetic points of view as proposed by other studies. For instance, external features, especially the body weight and tail length (Pan, 1998), gene frequencies (Melnick *et al.*, 1985; Weiss *et al.*, 1973), relatively short genetic distances

(Cronin, *et al.*, 1980), and similar allele-frequencies (Fooden *et al.*, 1989).

Genetic studies show that *M. nemestrina* has a close relationship with the Sulawesi macaques including *M. nigra* (Darga *et al.*, 1975; Cronin *et al.*, 1980; Melnick *et al.*, 1985). This study also demonstrates that *M. nemestrina* has a close relationship with *M. nigra* being in the same cluster. Species related to *M. nemestrina* have been considered to be the ancestor of Sulawesi macaques. A Sundland population may have entered Sulawesi, resulting eventually in the macaque radiation in Sulawesi (Delson, 1980; Fa, 1989; Fooden, 1969, 1975). A genetic study supports this hypothesis (Kamamoto, 1996).

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① 308-322

猕猴属种间颅骨差异的探讨

Q959.848

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摘要: 为了研究猕猴属的颅骨差异性, 从而探讨种间在形态、功能和系统分化方面的相互联系, 测定了 11 个猕猴种类的 77 个颅骨变量, 用于主成分分析和判别分析。应用巢式分析方法, 分析过程包括 3 个步骤。所有变量根据功能和部位的不同首先分为 7 个单位: 下颌、下颌齿、上颌齿、上面颅、下面颅、面颅后部和颅腔。第 2 步根据它们所揭示的相似性 (具有相同的种间及种内差异性类型) 合并为 3 个解剖区域: 咀嚼器官 (下颌、下颌齿、上颌齿)、面颅 (上面颅和下面颅) 和整个面颅后 (面颅后和颅腔)。第 3 步从 3 个解剖区域筛选出 27 个变量代表整个颅骨的形态结构。除了寻找不同的功能单位, 解剖区域及总的颅骨具有不同的种间和种内差异类型外, 此过程对筛出研究意义不大的变量起很重要的作用。上述分析过程分别用于对雌、雄性和两性的研究。所研究的 11 个猕猴种类间形成了 3 聚类。第 1 类包括食蟹猴 (*Macaca fascicularis*)、戴帽猴 (*M. sinica*) 和头巾猴 (*M. radiata*); 第 2 类包括猕猴 (*M. mulatta*)、熊猴 (*M. assensis*)、平顶猴 (*M. nemestrina*) 和黑猿 (*M. nigra*); 第 3 类包括猿猴 (*M. sylvanus*)、日本猴 (*M. fuscata*)、短尾猴 (*M. arctoides*) 和藏酋猴 (*M. thibetana*)。分别从两性差异、食物、生

态、分类和系统分化方面进行了差异性讨论。结果认为猕猴种间颅骨的差异性主要是由于系统分化不同而引起个体差异所致, 即种间和种内存在的个体差异。在主成分分析中, 这些差异在不同的区域表现在不同的成分上。在咀嚼器官上种间的差异在第 1 主成分上, 种内的差异则在第 2 主成分上。面颅的情况则刚好相反。这两种差异在面颅后及颅腔上则被第 1 和第 2 主成分所平分。这样, 种间的差异在咀嚼器官上大于种内的差异。种内的差异在面颅上则大于种间的差异。这两种差异在面颅后和颅腔上则几乎大小相等。这一研究结果表明, 与传统的概念不同, 第 2 主成分不仅仅表现形态、形状的差异, 而如同第 1 主成分一样, 也表现形态的大小成分。此研究所揭示的猕猴种间关系部分与 Foden (1976, 1980) 和 Delson (1980) 相同。如平顶猴与黑猿、短尾猴、藏酋猴和熊猴的关系。食蟹猴、头巾猴和戴帽猴的关系则不同, 并已得到有关分子生物学的支持, 此 3 种可能来自同一祖先并经历相同的扩散过程。此研究所设计的巢式分析过程提供了一种很好的差异性研究手段。最终结果暗示在形态学研究中仅仅考虑某一区域的形态结构是很不够的, 因为不同的部分具有不同的种间及种内差异类型。这在化石研究中尤其要注意。

关键词: 灵长类; 猕猴; 颅骨变异; 形态学; 功能适应性; 系统发育

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